

## CLADISTICS OF THE CHRYSIDOIDEA (HYMENOPTERA)

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*Abstract.*—A cladistic analysis of the relationships of the families of the Chrysidoidea is presented, and contrasted with the efforts of previous authors. The phylogenetic system here proposed is: Plumariidae is the sister-group of the other six families, which together form a monophyletic group. Scolebythidae is the sister-group of ((Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae)). Embolemidae and Dryinidae are sister-groups, and the closest relative of this component is the Sclerogibbidae. Bethylidae and Chrysididae are sister-groups, and together are the sister-group of Sclerogibbidae + (Embolemidae + Dryinidae). The monophyly of each of the families is established.

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Even recently, it has been common to state that no clear line can be drawn between Aculeata and the parasitic Apocrita (e.g., Malyshev, 1968; Evans and Eberhard, 1970; Richards and Davies, 1977). Traditional morphological *differentiae* such as trochanters one or two segmented, and hind wing jugal (sometimes termed anal) lobe present or absent are not consistently distributed. Even the sting has been stated to still function as an ovipositor in some of the aculeate families (e.g., Richards and Davies, 1977). This is scarcely possible given its anatomy, but the sting remained unstudied until recently in several key families. Discussion of the differences between the Parasitica and Aculeata has usually concentrated on behavior, with the Aculeata regarded as comprising mostly predatory forms. Thus the placement—and even composition—of the parasitic chrysidoid families has fluctuated between Parasitica and Aculeata in general treatments (e.g., Riek, 1970; Richards and Davies, 1977).

However, the adoption of cladistic methods has had a tremendous impact on ideas of phylogeny in the Aculeata. Oeser (1961), in a detailed phylogenetic study of the hymenopteran ovipositor, not only clearly established the monophyly of the Aculeata, but also identified a synapomorphy for Bethylidae + Chrysididae and showed a sister-group relationship between this group and the remainder of the Aculeata. This was followed by Brothers' (1975) analysis of 25 family-level taxa of Aculeata (cf. his fig. 2). While concentrating primarily on the Sclioidea *auct.*, Brothers provided the first detailed cladogram of the stinging Hymenoptera, and so put all subsequent investigations on a firm foundation. This is reflected in the works of Koenigsmann (1978) and Rasnitsyn (1980). Both these authors discussed the evolutionary relationships of the entire Hymenoptera, but, influenced by Brothers, treated Aculeata in greatest detail and presented their thoughts as critiques of his system. Both had substantial disagreements with Brothers, but none of these workers completely resolved the relationships of the chrysidoid families.

I have reanalyzed the relationships of the families of this group, and have reached different conclusions from previous authors. These results are summarized in Figure

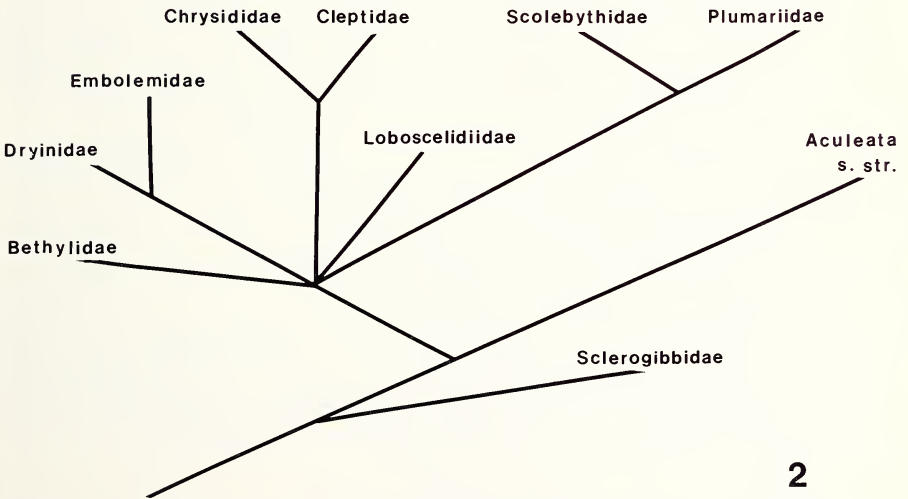
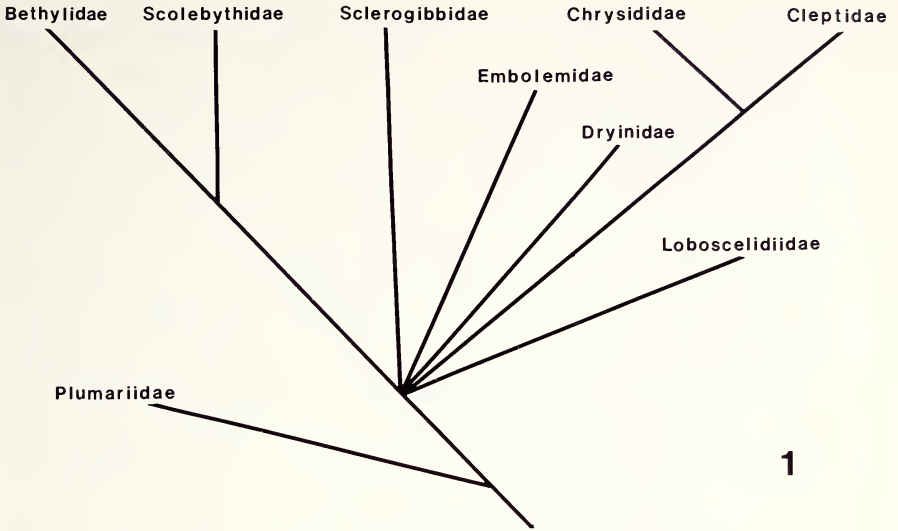
4. Below I present a brief summary of the recent systems suggested for the Chrysoidea, followed by the diagnoses (apomorphies; see Farris, 1979) for my cladogram, and discussion of the characters. This is the first complete cladistic analysis of the relationships among chrysidoid families.

#### RECENT HYPOTHESES

Brothers (1975) did not examine all the chrysidoid families. He considered Plumariidae and Scolebythidae separately, and lumped Bethylidae, Chrysididae, Cleptidae (a subfamily of Chrysididae, cf. Krombein, 1957; Day, 1979; Bohart and Kimsley, 1982) and Dryinidae into a "bethylid group" in his analysis. He stated that Sclerogibbidae, Embolemidae and Loboscelidiidae (a subfamily of Chrysididae, cf. Day, 1979), which he did not see, were considered to belong to the bethylid group. His cladogram for the taxa he actually studied (1975:fig. 2) placed Plumariidae as the sister-group of Scolebythidae + the "bethylid group." However, his figure 67, including all the aculeate families, showed Scolebythidae and Bethylidae as sister-groups, placing the remaining "bethylid group" families in an unresolved polychotomy. This is reproduced here as Figure 1. Brothers' legend (1975:588) indicated that these relationships within the Chrysoidea (termed by him Bethyloidea) were based on "personal impressions."

Koenigsmann (1978) presented essentially a critical literature review. He followed principles of phylogenetic reasoning, but did not himself examine specimens of all the taxa. Consequently he was unfamiliar with some of the characters, which resulted in occasionally superficial treatment. He removed Sclerogibbidae from the Chrysoidea and placed it as the sister-group of the entire Aculeata, primarily based on heavily weighting 13-segmented antennae. This was the only synapomorphy for his Aculeata, and of course implied that the multisegmented antennae of sclerogibbids was the primitive condition. He pointed out that possession of the crucial autapomorphies of the Aculeata, the sting characters, remained to be demonstrated for sclerogibbids, but averred that they could not be placed in the Parasitica. He alluded to the possibility of the multisegmented antennae of the Sclerogibbidae being secondary, and mentioned in passing the similarity of the wing venation groundplans of this family and the Chrysoidea (termed by him Bethyloidea). Koenigsmann's suggested relationship represents a radical departure from the tradition, extending back to Ashmead (1902) and Kieffer (1914), of considering Sclerogibbidae as close to Bethylidae. Within this restricted Chrysoidea, he depicted the relationships as mostly unresolved (see Fig. 2), but did indicate the following sister-groups: Embolemidae + Dryinidae (based on 10-segmented antennae and a tibial spur formula of 1-1-2), Chrysididae + Cleptidae (various characters, including the tubelike ovipositor) and Scolebythidae + Plumariidae (based on absence of a pronotal collar, a character mentioned by Brothers, 1975).

Rasnitsyn (1980), by contrast, provided some new data. He rejected cladistics (terming it a "sterile trend" on p. 7 of the original text), and proceeded largely by attempting to draw smooth transitions between taxa (for example, his discussion of the placement of Miomoptera on p. 38 of the original). This is unsurprising given his paleontological background, but at least he dealt with characters to the extent



Figs. 1, 2. 1. Cladogram of the Chryridoidea, after Brothers (1975:fig. 67). 2. Cladogram of the Chryridoidea, after Koenigsmann (1978:fig. 4).

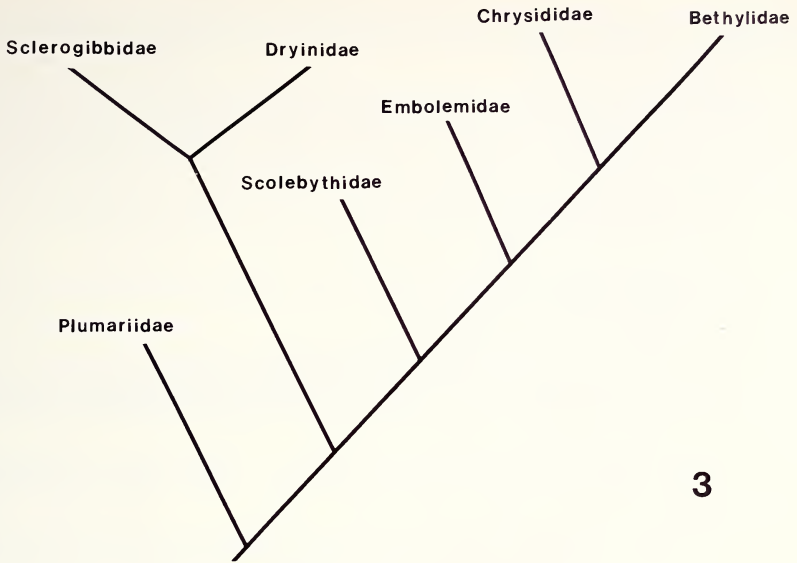
that he rejected some of Brothers' and framed his discussion of aculeates in terms of alternative character interpretations. He figured (1980:fig. 147f) the first dissection of the sting of a sclerogibbid, as well as illustrating stings of the other chrysidoid families (except Plumariidae). His cladogram (here as Fig. 3) grouped Bethylidae + Chrysididae, based on the loss of the articulation between the second valvifer and second valvulae of the sting, as first noted by Oeser (1961). But he then grouped Embolemidae as the sister-group of this component. He first stated that the antennae of embolemids and dryinids were different in structure (not geniculate and scape long vs. "often" geniculate and scape short; pedicel/flagellum articulation fixed vs. mobile). He dismissed the shared homopteran hosts by arguing that the host habitats were different, and that the "confined" hosts of embolemids were similar to those of Bethylidae + Chrysididae in habitat. He stated that the endoparasitism of embolemids (Bridwell, 1958) found its "analogy among Aculeata only in Chrysididae." Finally, he noted that embolemids and dryinids both lacked a furcula in the sting, but considered the elongate base of the second valvulae in Embolemidae, which is compressed into a vertical lamella (Rasnitsyn, 1980:fig. 147b), to resemble the unpaired part of the furcula in Bethylidae and perhaps to be homologous with it.

Besides these arguments, he advanced two characters as synapomorphies for Embolemidae + (Bethylidae + Chrysididae). These were the metasternum and the articulation between metasomal sterna I and II. He considered the metasternum of Bethylidae to be derived (Brothers, 1975, treated it as plesiomorphic in Aculeata) and the median carina of embolemids and chrysidids to be either a precursor or rudiment of it. He characterized the articulation between metasomal sterna I and II in these three families as with a "primarily" thick, straight margin to I (secondarily with membranous lobes and median notches in Chrysididae); and a straight margin to II, with small lateral notches and edges invaginated with desclerotized areas (notches and desclerotized areas large and edges little invaginated in Chrysididae).

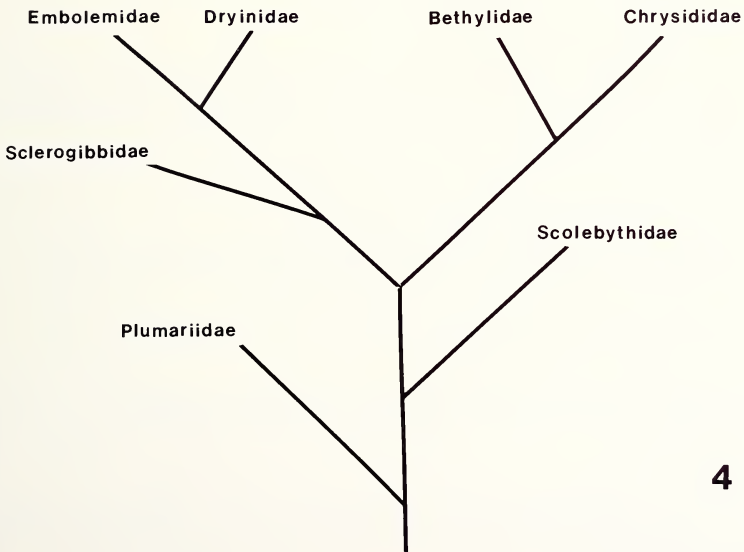
Among the remaining families, he suggested a sister-group relationship between Sclerogibbidae and Dryinidae. This was supported by: 1) metasomal sternum II with median notch and expanded acrosternite; 2) elongate base of the second valvulae, although "the process thus formed differs in shape"; 3) enlarged foretarsal claws in the female (he noted that only one unguis was enlarged in only some dryinids, so this was "a common tendency"); 4) ectoparasitism of active non-Holometabola hosts. He characterized the Scolebythidae and Plumariidae as "the earliest groups to diverge off the common stem of Chrysidoida," but did not draw any conclusions about which came off first or the relationships of his four main chrysidoid components to one another (although his cladogram was completely resolved; here as Fig. 3). It will be shown below that most of Rasnitsyn's conclusions are not tenable.

#### GROUNDPLAN DIAGNOSES

This section lists the *inferred* autapomorphies for each component and term (*sensu* Nelson, 1979: components are branch points and terms are terminal taxa) of the cladogram of Figure 4. The states are those of the groundplan of each group, and may have been further modified in individual members of a component or term. Justification of these interpretations is deferred to the following section, along with



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Figs. 3, 4. 3. Cladogram of the Chrysidoidea, after Rasnitsyn (1980:fig. 38). 4. Cladogram of the Chrysidoidea, according to the present work.

discussion of characters mentioned by previous authors but not found to be useful in this study.

*Chrysoidea* Latreille, 1802

Reduction in venation: fore wing with eight cells (third discoidal and third submarginal lost by reduction of  $m-cu_2$  and  $r-m_3$ ). Hind wing with veins 2A, 3A and jugal lobe lost.

Loss of metathoracic-propodeal suture ventral to the endophragmal pit.

Articulation within the second valvifer of the sting.

*Plumariidae* Brues, 1924 (1914)

Palpal formula 6:3 (5:3 in females).

Prosternum with posterior surface depressed.

Male metasternum entirely depressed below level of mesosternum.

Female wingless, pronotal collar reduced, and mesosoma modified in connection with aptery.

*Scolecbythidae* + ((*Sclerogibbidae* + (*Embolemidae* + *Dryinidae*)) + (*Bethylidae* + *Chrysididae*))

Fore wing with seven closed cells (loss of second submarginal due to loss of  $r-m_2$ ),  $RS_2$  vein lost.

Hind wing venation reduced: all cells, all crossveins and M+Cu vein lost.

*Scolecbythidae* Evans, 1963

Prosternum enlarged.

Pronotal collar reduced.

Forecoxae posteriorly produced.

(*Sclerogibbidae* + (*Embolemidae* + *Dryinidae*)) + (*Bethylidae* + *Chrysididae*)

Palpal formula 6:3.

Metapostnotum constricted.

*Sclerogibbidae* + (*Embolemidae* + *Dryinidae*)

Hind wing with veins SC+R+RS and 1A lost.

Furcula lost, elongate base of second valvulae forming lamellate process.

*Sclerogibbidae* Ashmead, 1902

Antennae with more than 14 segments.

Palpal formula 5:3.

Female wingless, with subcordate head and fore femora enlarged.

Hosts Embiidina.

*Embolemidae* + *Dryinidae*

Fore wing with six closed cells (first submarginal lost due to reduction of RS).

Antennae 10-segmented.

Loss of one mid-tibial spur.

Hosts Homoptera Auchenorrhyncha.

Endoparasitic in first instar and later protruding from host.

*Embolemidae* Foerster, 1856

Antennal prominence.

Female palpal formula 4:2.

Fore tibial calcar strongly curved and truncate.

*Dryinidae* Haliday, 1833

Fore wing with five closed cells (loss of discal cell due to reduction of m-cu<sub>1</sub> and RS+M).

*Bethylidae* + *Chrysididae*

Loss of articulation between second valvulae and ventral part of second valvifer.

*Bethylidae* Haliday, 1839

Head capsule modifications associated with prognathy.

Clypeus with longitudinal median carina.

Metasternum anteriorly broad.

*Chrysididae* Latreille, 1802

Fore wing with six closed cells (first submarginal lost due to reduction of RS).

Palpal formula 5:3.

Female with four visible metasomal terga, male with five.

Type of articulation between metasomal sterna I and II.

Ovipositor tube.

## CHARACTER ANALYSIS

*The wings*

The wing venation has not generally been used in the higher-level taxonomy of the Chryridoidea. Brothers (1975) considered the reduction in the number of cells in the hind wing to be "probably significant" in associating Scolebythidae with his "bethylid group," and loss of the hind wing jugal lobe has long been used as a distinguishing feature of the superfamily. But aside from this, the wings have probably been considered more often a source of difficulty than a source of characters. This is due to apparently similar patterns of reduction appearing in many groups (including other Hymenoptera), a situation that traditional taxonomy is ill-equipped to deal with. When cladistic analysis, with its emphasis on similarity in groundplans, is applied to the venation, a more coherent pattern emerges.

In this discussion, only convex, pigmented veins are treated. In many of the instances of extensive reduction, the veins may be indicated by traces, that is unpigmented lines or creases. The term "reduced" is used to indicate veins reduced to such traces or completely lost. In the terminology of Mason (1986a), these traces are "spectral" veins, which may evanesce over their course. Mason (1986a) recognized two other, prior stages in the reduction of convex, pigmented veins: "tubular" for those with sharply defined edges, and "nebulous" for those with ill-defined edges. Nebulous veins are here considered as not reduced. However, it should be noted that the transition to spectral veins may be gradual.

*Fore wing.* The groundplan number of closed cells in the fore wing of Aculeata is

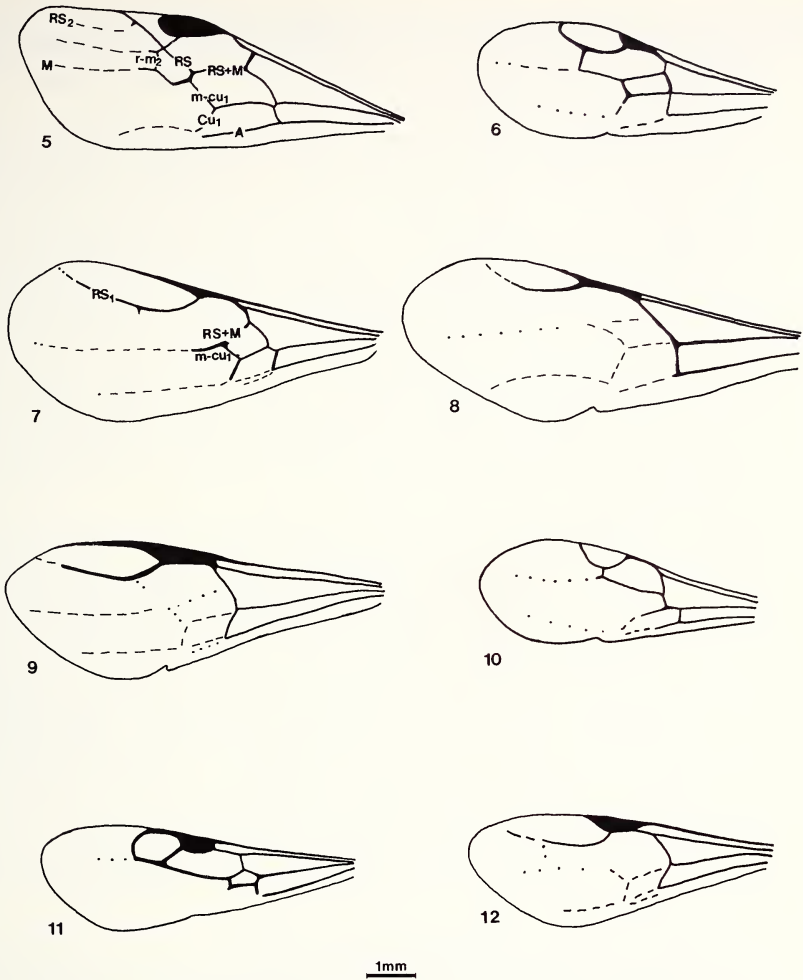
considered to be ten (Brothers, 1975). This is the number in the Aculeata s. str. (Sphecoidea + Vespoidea, *sensu* Brothers, 1975), the sister-group of the Chryridoidea. The evolution of the venation in chrysidoids is a history of progressive reduction from this plesiomorphic state. The maximum number of cells in the Chryridoidea is eight, found in the Plumariidae (Fig. 5), which may be inferred to be the groundplan condition in the superfamily. As such, it is an autapomorphy of the group. This state is a product of the loss of the  $m-cu_2$  and  $r-m_3$  crossveins, compared to the sister-group, which results in the loss of the third discoidal (2M) and third submarginal (2RS) cells, respectively.

All Chryridoidea, aside from Plumariidae, also lack the second submarginal cell (1RS), due to the loss of the  $r-m_2$  crossvein (Figs. 6–12). Further, they lack the  $RS_2$  vein, present as a spur on the marginal cell in plumariids (Koenigsmann, 1978, and Rasnitsyn, 1980, considered this an apomorphic *de novo* vein; Day, 1977, adopted the interpretation followed here). These states are therefore synapomorphies of the six families. From this condition there has been further extensive reduction, ranging to only one closed cell (in aphelopine dryinids, Loboscelidiinae and some bethylids). However, the pathways of reduction have been different in most of the groups and the resultant patterns differ in detail.

Embolemids and chrysidids have six cells in the groundplan (Figs. 7, 8). They lack the first submarginal cell due to reduction of the RS vein. This is also true of dryinids, but that family has only five cells in the groundplan (Fig. 9); they lack also the discal (1M) cell, due to the loss of the  $m-cu_1$  crossvein and reduction of the RS+M vein. In those dryinids with apparent RS and  $m-cu_1$  these are spectral veins (Fig. 9; some *Deinodryinus*, where RS may appear nebulous in part; *Thaumatodryinus*). Reduction to six cells by loss of the first submarginal is here interpreted to be a synapomorphy of the Embolemidae + Dryinidae, with further loss of the discal cell an autapomorphy of the Dryinidae. The state of reduction of the first submarginal cell is also found in Chrysididae as a groundplan character. This must be inferred to be convergent, as both sclerogibbids (Fig. 10) and some bethylids have this cell (Bethylineae: Fig. 11, *Eupsenella*, where it is closed by tubular veins; in *Lytopsenella*, it is closed by nebulous veins, cf. Evans, 1964). Other bethylids (including Mesitiinae) have RS+M and  $m-cu_1$  reduced to spectral veins or completely lost, and so the question arises as to whether the appearance of these veins in bethylines is secondary. However, Evans (1964) treated bethylines as relatively primitive (cf. his fig. 1), and thus the interpretation of presence of the first submarginal in the bethylid groundplan under present knowledge is better supported.

From these states further reductions have occurred within families, but as they do not pertain to the groundplans they are not important for family level relationships. The  $Cu_1$  and A veins are nebulous in most groups (Figs. 6–10, 12), and may be distally reduced so that the second discoidal cell appears open (Figs. 5, 6, 8). This state also occurs in the plumariid *Myrmecopterinella* (Day, 1977), which has additionally lost the second submarginal cell. The marginal cell is closed only by a distally nebulous  $RS_1$  vein, which may become spectral, in many groups (Figs. 7–9, 12). Although the groundplan state in dryinids is five closed cells, most species have fewer. The second discoidal, submedian ( $M+Cu_1$ ) and median (R) cells may be lost and





Figs. 5-12. Fore wings of Chrysoidea. 5. *Plumarius* (Plumariidae). 6. *Ycaploca evansi* (Scolebythidae). 7. *Embolemus* (Embolemidae). 8. *Cleptes semiauratus* (Chrysididae). 9. *Tri-dryinus poecilopterae* (Dryinidae). 10. *Sclerogibba* (Sclerogibbidae). 11. *Eupsenella* (Bethylidae). 12. *Pristocera armifera* (Bethylidae). —: tubular vein; - - -: nebulous vein; ·····: spectral vein.

the marginal cell may be open (cf. Olmi, 1984). The discal cell is absent in the sclerogibbid *Probethylus*, as well as some species of *Sclerogibba* (Fig. 10). Many chrysidids have only three cells closed by tubular or nebulous veins; the marginal cell is open and the discal and second discoidal cells are lost. In *Loboscelidia* only the median cell is closed. Finally, no bethylid actually has seven closed cells. The

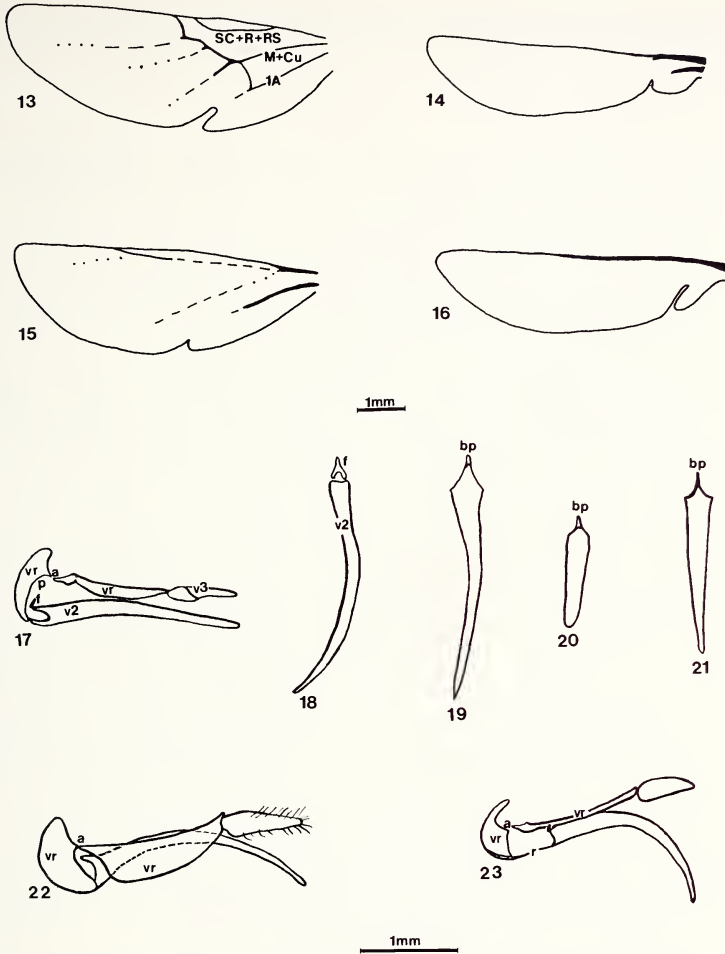
marginal cell is often open, and the first submarginal, discal and second discoidal cells absent. The first submarginal and discal cells are present only in some Bethylinae (Fig. 11) and the second discoidal cell closed, by nebulous veins, in Pristocerinae (Fig. 12). One or two closed cells occurs in Epyrinae.

*Hind wing.* The primitive number of cells in the hind wing of Aculeata is three (Brothers, 1975), the number found in Sphecoidea + Vespoidea, and Ichneumoidea, the sister-group of the Aculeata (Mason, 1986b). Veins 2A and 3A are present in addition to a jugal lobe (Brothers, 1975). All Chrysidoidae lack veins 2A and 3A and the jugal lobe. These developments are autapomorphic in the superfamily, although they have occurred elsewhere in the Aculeata (Brothers, 1975). Rasnitsyn (1980) questioned whether absence of a jugal lobe in chrysidoids was not actually plesiomorphic, "since Karatavitidae are so far the only Jurassic forms of the Apocrita in which the jugal lobe has been found, and we have no grounds to assume its presence in the ancestor of the Aculeata." On the contrary, since a jugal lobe is found also in Symphyta (and veins 2A and 3A) and Evanioidea, there is certainly reason to consider its presence in Aculeata (a relatively primitive group of Apocrita; Mason, 1986b) as plesiomorphic.

Compared to Plumariidae (Fig. 13), the remaining Chrysidoidae have derived hind wing venation. All crossveins and vein M+Cu are lost. The costa is distally reduced, and SC+R+RS and 1A are the remaining longitudinal veins (Fig. 14). There are no closed cells, except for the costal in some Chrysididae (Fig. 15). Brothers (1975) treated this presence as the primitive condition in his "bethylid group," but it is here considered as a secondary reversal in chrysidids. This is the parsimonious interpretation, for if it were plesiomorphic in Chrysidinae then the costal cell must be inferred to have been convergently reduced at least nine times (scolebythids, sclerogibbids + embolemids + dryinids, bethylids, Cleptinae, Amiseginae + Loboscelidiinae, Elampinae, Parnopinae, Allocoeliinae and within Chrysidinae; cf. Bohart and Kimsey, 1982:fig. 1, for a cladogram of chrysidid subfamilies). The case for reversal is therefore strong. A similar interpretation is here applied to the M+Cu vein (only *distally* tubular) present in a few Chrysidinae (*Stilbum*) and Cleptinae (distally nebulous, Fig. 15).

From the inferred primitive longitudinal vein complement of SC+R+RS, 1A and a distally reduced C, the Sclerogibbidae + (Embolemidae + Dryinidae) are further derived in lacking SC+R+RS and 1A (Fig. 16). This is a synapomorphy of these families. SC+R+S has also been distally reduced in some Bethylidae + Chrysididae.

*Brachyptery.* Reduction or loss of the wings has occurred numerous times in the female sex in Chrysidoidae. Males are sometimes micropterous (Dryinidae, see Olmi, 1984; Bethylidae, Evans, 1964) or apterous (Chrysididae, Krombein, 1957). That these are independent is attested to by the different modifications of the mesosoma associated with brachyptery in the different groups (reviewed by Reid, 1941, and see Evans, 1966, and Brothers, 1975). Brachyptery is characteristic of female Plumariidae and Sclerogibbidae. It is autapomorphic in each of these groups. Reid (1941) stated that all female Embolemidae are brachypterous or short-winged, but fully winged females occur in *Ampulicomorpha confusa* as well as various undescribed species. It is also found in some Dryinidae (within Anteoninae, Bocchinae, Gonatopodinae



Figs. 13–23. 13–16. Hind wings of Chrysididae. 13. *Plumarius* (Plumariidae). 14. *Eupsenella* (Bethyidae). 15. *Cleptes semiauratus* (Chrysididae). 16. *Embolemus* (Embolemidae). 17. *Clystopenella longiventris* (Scolebythidae). Lateral view of sting apparatus. Tergum IX, first valvifer and first valvulae not shown. 18–21. Oblique ventral view of second valvulae (sting). 18. *Plumarius* (Plumariidae). 19. *Probethylus callani* (Sclerogibbidae). 20. *Ampulicomorpha confusa* (Embolemidae). 21. *Tridryinus poecilopterae* (Dryinidae). 22–23. Lateral view of sting apparatus. 22. *Probethylus callani* (Sclerogibbidae). 23. *Pristocera armifera* (Bethyidae). a: articulation between dorsal and ventral arms of second valvifer; bp: basal process of second valvulae; f: furcula; p: postincision; r: ramus of first valvula (lancet); v2: second valvulae (sting); v3: third valvulae (gonostylus); vr: second valvifer.

and Apodryininae), Bethyridae (within each subfamily) and Chrysididae (within Amiseginae). In itself, it is evidently not significant, nor are the associated modifications generally even family characters.

### Head

*Head shape.* The most distinctive aspect of the bethylid facies is prognathy. Its appearance in the female has been used as the key character of the family (Koenigsmann, 1978), although Mesitiinae are then considered a problem, as they are stated to be orthognathous (Moczar, 1970; Koenigsmann, 1978; Nagy, 1969 actually termed them hypognathous!). This character has not been studied carefully. There is variation in the trait; it is exaggerated when the head is elongate, as in *Pristocera* females. The genal bridge (found throughout Chrysidodea) is expanded, and ventrally comprises half or more the length of the head. The postgenal bridge is also expanded, and is often still separated from the genal bridge by the occipital carina. The temples and upper face are lengthened relative to the rest of the head, and the proboscoidal fossa shortened in the extreme condition. The eyes are usually situated very close to the mouthparts, and occupy relatively little of the lateral surface area of the head, typically less than half the length of the head capsule, and may be greatly reduced in genera such as *Pristocera*. The elongation of the genal and postgenal bridges, and the relatively small eyes obtain regardless of the orientation of the mouthparts, which is a relatively unimportant feature. Due to these characters most bethylids are prognathous to some extent—including males and Mesitiinae. To be sure, the development of “prognathy” in the females of the subfamilies Pristocerinae, Epyrinae and Bethylinae is usually greater than that in males and Mesitiinae, but is a matter of degree and does not appear in all species. For example, in *Goniozus* the eyes are larger relative to the rest of the head, and the mouthparts less prognathous than Mesitiinae. For present purposes it is enough to establish that Bethyridae are apomorphic in their type of head capsule relative to the rest of the Chrysidodea, particularly the cleptine and amisegine chrysidids, to which Mesitiinae have often been likened (Ashmead, 1902; Reid, 1941; Nagy, 1969; Moczar, 1970). In chrysidids, the genal bridge is often similarly elongate, although the mouthparts are orthognathous. The postgenal bridge is not so elongate, but the most significant difference compared to bethylids is that the eyes cover most of the lateral surface of the head—the temples are practically nonexistent. In general other Chrysidodea have the eyes relatively larger than in bethylids. The female plumariid I have seen has relatively small eyes and a broad genal bridge with prognathous mouthparts, but the postgenal bridge not so well developed. The eyes may be relatively small and the mouthparts somewhat prognathous in scolebythids (*Ycaploca*, where the head in lateral view even appears to have the oblong shape characteristic of the highly derived bethylids). But the genal bridge is not so broadened and the proboscoidal fossa is larger. The mouthparts are somewhat prognathous in sclerogibbid females and some dryinids, but again the details of the head shape are different. Sclerogibbids have rather elongate eyes and the postgenal bridge not well delimited, and dryinids have the eyes relatively larger and the hypostoma enlarged when prognathous. The genal bridge is not as broad, and this is also true in embolemid, where the eyes may be relatively small.

There are thus numerous modifications of the head shape, and each of the chrysidoid families could perhaps be said to have some apomorphies. The orientation of the mouthparts *per se* is not important. A broad genal bridge is common, but bethylids are unique in combining that with a broad postgenal bridge and primarily relatively small eyes—and often with prognathous mouthparts. Mesitiinae are not similar to Chrysididae in head characters, and as discussed below, are only superficially similar in other features. Among the remaining families, the sclerogibbids have the most outstanding apomorphy: the subcordate female head (figs. in Krombein, 1979). The posteriad projection of the vertex, bordered by broad flattened setae (Krombein, 1983), in Loboscelidiinae is also remarkable.

*Clypeus.* In the Chryridoidea the clypeus is usually quite short and transverse, a state Brothers (1975) concluded is primitive in Aculeata. Bethylidae have an autapomorphy of the clypeus: a longitudinal basomedian carina. The length and height of the carina vary (figures in Evans, 1978); it may be continuous with a frontal carina proceeding dorsad of the antennae (e.g., *Goniozus*) or laterally dilated (*Mesitius apterus*, fig. 11 in Moczar, 1970). It is absent secondarily in some epyrines and bethylines (e.g., figs. in Evans, 1978), but is present in the great majority of taxa. The clypeus is variously modified in chrysidids but not carinate. A *frontal* carina is present in some amisegines (*Alieniscus*, Krombein, 1957) but in general the front is excavated in chrysidids.

*Antennae.* Characters of the antennae have played a prominent role in discussion of the taxonomy of Chryridoidea. In particular, the number of segments has been frequently discussed. Sexual dimorphism in the antenna segmentation is an autapomorphy of the "Aculeata s. str." (Brothers, 1975; Koenigsmann, 1978; Rasnitsyn, 1980). The 12-segmented antennae in the female is considered a reduction from 13 segments, found in males and most Chryridoidea (as well as many Parasitica). The groundplan number of 13 segments is in turn a reduction from the multisegmented antennae of other Macrohymenoptera (Ichneumonoidea, the sister-group of Aculeata; Mason, 1986b). The Sclerogibbidae are then a problem, for their antennal segment number ranges from 15 (a female *Probethylus* from Texas I have seen) to 39 (Richards, 1958). Koenigsmann (1978) therefore placed this family as sister-group to the entire Aculeata. However, the number of segments varies not only between and within sexes of the same species (Richards, 1939b; Shetlar, 1973; Krombein, 1979; pers. obs.) but within the same individual (Richards, 1939b). This instability can be considered to provide support for the interpretation of secondary increase, and reversal is required in any event in view of the chrysidoid autapomorphies that sclerogibbids possess (contrary to Koenigsmann, 1978).

The number of segments has not only increased during the evolution of the Chryridoidea, it has decreased in some groups. The number is 12 in both sexes of some bethylids (Evans, 1964) and at least the male of *Myrmecopterella* (Plumariidae; Day, 1977). And the number is 10 in both sexes of Embolemidae + Dryinidae. This state is usually taken to indicate recent common ancestry for these two families (Koenigsmann, 1978), however Rasnitsyn (1980) considered the number to be convergent. He stated that the antennae in these two families were markedly different in structure, often geniculate and with a short scape and mobile pedicel/flagellum

articulation in Dryinidae vs. not geniculate and with a long scape and fixed pedicel/flagellum articulation in Embolemidae. He stated: "It is therefore doubtful that their resemblance has been inherited." His argument would have benefitted from application of cladistic logic, for no such conclusion follows if one of these states is plesiomorphic. Such is in fact the case. Geniculate antennae are not characteristic of all members of any chrysidoid family, being absent in Plumariidae, Scolebythidae, Sclerogibbidae, various Bethylidae and loboscelidiine chrysidids as well as most Dryinidae. Geniculate antennae are certainly not characteristic of the dryinid groundplan, and so the two families do not differ in this character. An elongate scape (as long or longer than the head) and fixed pedicel/flagellum articulation are certainly derived; they are only approached elsewhere in Chrysoidea in Loboscelidiinae. Dryinidae are therefore plesiomorphic in these states and Embolemidae autapomorphic, and relationship is not precluded by this.

Besides the structure of their antennae, Embolemidae are autapomorphic in the antennal prominence. The face is drawn out into a conical projection supporting the antennal sockets, and the entire head appears pyriform, with the frontoclypeal suture well separated from the antennal sockets.

*Palpi.* The number of segments in the palpi has traditionally been of use in the generic and specific taxonomy of several chrysidoid families (Chrysididae, Bohart and Kimsey, 1982; Bethylidae, Evans, 1964; and especially Dryinidae, Olmi, 1984). Reductions from the primitive state of 6-segmented maxillary and 4-segmented labial palpi (Brothers, 1975) range to complete absence of the labial palpi (e.g., *Myrmecopterina*, Plumariidae). The primitive formula is retained in Scolebythidae, and had also been considered part of the plumariid groundplan (present in male *Heterogyna*; Brothers, 1974, 1975). However, Day (1984, 1985) established that *Heterogyna* is a sphecid. The groundplan formula in Plumariidae is therefore 6:3 (5:3 in the female), an autapomorphy. The formula of 6:3 is also a synapomorphy of (Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae). Further reductions characterize the groundplans of Sclerogibbidae and Chrysididae (to 5:3) and Embolemidae (4:2 in the female).

#### *Mesosoma*

*Pronotum.* Brothers (1975) considered a pronotal "collar," an anterior projection covering the propleura dorsally, to be plesiomorphic in the Aculeata, as that is generally the condition in other Hymenoptera. Absence of this collar, so that the propleura are dorsally exposed, he considered separately derived in Scolebythidae and plumariid females. Koenigsmann (1978) used reduction in the collar as his synapomorphy for Plumariidae and Scolebythidae. However, as realized by Brothers (1975:502), the derived state was attained by different modifications in the two groups. Male plumariids do have a relatively short collar. In plumariid females the collar is absent, and the pleura are fused both dorsally and ventrally, forming a rigid tube (Evans, 1966:fig. 11). The pronotum is enlarged relative to the rest of the thorax, a common modification in wingless chrysidoid females (Reid, 1941:figs. 42-54). In scolebythids the pleura are simply produced anteriorly; no pronotal modification or pleural fusion occur. The collar is also absent in some other wingless female chry-

sidoids, e.g., *Pseudogonatopus*. Therefore there is little doubt that the loss of the collar is convergent, and not very similar, in the two groups.

*Prosternum.* Evans (1963) in his description of Scolebythidae, noted that the large prosternum was an unusual character in Hymenoptera. The propleura are widely separated posteriorly, and the sternum flat. Brothers (1975) called this the primitive extreme, but also stated "Since this condition is more extreme than in any other taxon, it may be a secondary development." This is most likely the case. Only the uniform plane of the prosternum is plesiomorphic. Thus the prothorax of scolebythids is highly modified, for in addition to the reduced pronotal collar, divergent pleura and enlarged prosternum, the coxae are also apomorphic. They are basally separated but produced posteriorly beyond the trochanteral insertions so that they are contiguous apically, a unique condition in Aculeata (Brothers, 1975).

Evans (1973) described the Cretaceous *Cretabythus* as a doubtful scolebythid. The single specimen was stated to have the prosternum "not evident," in addition to having a short pronotal collar. The fore coxae were described as contiguous, but no further details were given. The wing venation appears to be that of a scolebythid, but as the prothoracic modifications are the crucial autapomorphies of the family, it is possible that this assignment is incorrect. If the placement is upheld, it conclusively establishes the secondary nature of the prothoracic characters of extant Scolebythidae.

Depression of the prosternum is an autapomorphy of the Plumariidae (Brothers, 1975). The prosternum has only the anterior part visible, the posterior part being depressed in a different plane from the rest of the sternum. In other chrysidoids the prosternum is in a uniform plane when visible (it is very reduced in embolemid and sclerogibbids), as is also the case in ichneumonoids.

*Fore legs.* The apomorphic production of the coxae in scolebythids has been alluded to previously. Additional characters include the enlarged femora in sclerogibbids, and the tarsal chela of dryinids. The fore femora are larger than those of succeeding legs in both male and female sclerogibbids, but are enormously swollen in females (see fig. 2 in Krombein, 1979). This is one of the most recognizable traits of the family, and is an outstanding autapomorphy. The femora are often enlarged in females of other Chryridoidea (Bethyidae, Embolemidae, Dryinidae) but not to the same degree nor more than succeeding legs (exception in Bocchinae). The chela formed by the fifth tarsal segment and one enlarged unguis of female dryinids is an adaptation for seizing the host prior to oviposition. Other modifications of the fore legs are associated with its development (Richards, 1939a). It is not found in females of the subfamilies Aphelopinae and Biaphelopinae, therefore it is not a groundplan feature of the Dryinidae. Rasnitsyn (1980) listed enlarged unguis of the anterior tarsi in females as a synapomorphy of Sclerogibbidae and Dryinidae, but noted that only one unguis was enlarged in only some dryinids, and so this was a "common tendency" rather than a common character. It is worth pointing out that even this is incorrect; the claws of the two families are not at all similar. The unguis of sclerogibbids are not enlarged; the arolium is. The unguis are no larger than those of any other chrysidoid, but the expanded arolium is autapomorphic. In dryinids with the chela, the arolium is elongate and the orbicula well-sclerotized and covering most of the

dorsal surface. Aphelopinae and Biaphelopinae have plesiomorphic claws (Olm, 1984).

*Tibial spurs.* The plesiomorphic spur formula is 1-2-2 in Aculeata (Brothers, 1975). This is the condition in most Chrysoidea. The formula is 1-1-2 in Embolemidae + Dryinidae, one mid tibial spur having been lost. This is a synapomorphy of the two families (Koenigsmann, 1978). There has been further reduction in some Dryinidae, to no mid tibial spurs in some groups (list in Olm, 1984).

Koenigsmann (1978) also listed the fore tibial spur as a possible autapomorphy of the Embolemidae. The calcar is short, strongly curved and has a strongly truncate apex in female embolemids. The state in other chrysoids is generally that which Brothers (1975) considered plesiomorphic in Aculeata, namely more or less straight and with an acute apex.

*Metasternum.* Brothers (1975) considered a metasternum with the mesal section in approximately the same plane as the mesosternum, and the lateral thirds depressed to accommodate the mid coxae, to be primitive in Aculeata. The basis for this interpretation was "because this is the condition in various aculeates that are considered to be the most primitive on the basis of other characters." The state with the metasternum depressed anteriorly and laterally so that the mid coxae are nearly contiguous he considered apomorphic, and the state of the metasternum completely depressed further derived from this. These latter two states are only found within Plumariidae (female and male, respectively) in the Chrysoidea.

Rasnitsyn (1980) disputed this hypothesis, but he did not characterize it completely correctly. He considered a metasternum with "its middle portion raised in the form of a clearly demarcated platform forcing the mesocoxae widely apart," as in Bethyloidea, to be apomorphic. A median carina on the metasternum in Embolemidae and Chrysoidea (with two carinae in Cleptinae) "may be the precursor or rudiment of the broad platform." Rasnitsyn further stated that according to Brothers a platform is present in female plumariids, which Brothers did not indicate, and that in other Chrysoidea the metasternum is more or less flat, without a platform or carina. The platform Rasnitsyn reasoned to be apomorphic because: 1) it "probably was not developed as yet" in the Jurassic Bethyloidea, which he treats as the ancestor of Aculeata; and 2) it is absent in Sclerogibbidae and ants, "many of which are close in their mode of preying (inside the substratum) to the forms furnished with a platform." Therefore it developed secondarily, because Rasnitsyn believed prey searching in the substrate to be primary for Aculeata.

It is probable that the anteriorly broad metasternum found in Bethyloidea is in fact apomorphic. The metasternum is usually anteriorly narrow in other Chrysoidea, primitive Sphecoidea and Ichneumonoidea. The sternum is not differentiated into approximate thirds, and is depressed anterolaterally in many ichneumonoids. It is therefore probably most parsimonious to regard an anteriorly narrow metasternum in approximately the same plane as the mesosternum as plesiomorphic for Aculeata (Brothers' state 38.1), including female Plumariidae. Then a raised (i.e., anteriorly broad) metasternum is separately derived in the Bethyloidea and some Vespoidea (Brothers, 1975, state 38). Some chrysoids (Cleptinae) also have an anteriorly broad sternum, but as most do not, and a broad sternum and carinae may be found in members of other families (e.g., Dryinidae), this appears to be convergent. Embo-



lemids and chrysidids in general are no more similar to bethylids in the metasternum than are scolebythids, sclerogibbids or dryinids. The contention that the carinae of Embolemidae and Chrysididae are homologous with the anteriorly broad sternum of bethylids is unfounded; there is no logical reason for one state to be a transformation of the other. Finally, under this interpretation, the completely depressed metasternum of male Plumariids is autapomorphic, a state also found in some Vespoidea (Brothers, 1975).

*Metapostnotum.* Obliteration of the metapostnotal-propodeal suture and reduction of the metapostnotum to lateral remnants only was used by Brothers (1975) as a synapomorphy for Scolebythidae and his "bethylid" group. This suture is still visible in male Plumariidae. However, as pointed out by Rasnitsyn (1980), the suture is present in *Ycaploca*, a scolebythid not seen by Brothers (and also in the putative fossil scolebythid *Cretabythus*). Rasnitsyn also claimed that "the posterior boundary of the metapostnotum also persists in primitive Dryinidae (Aphelopinae and Anteoninae)." The suture is not present in any members of these subfamilies that I have examined, and Olmi (1984) makes no reference to this suture in any dryinid. Also, Olmi's figures of Aphelopinae, Biaphelopinae and Anteoninae do not show this suture. Therefore I regard Rasnitsyn's statement as an error, and treat constriction of the metapostnotum as a synapomorphy for (Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae). This state is convergently derived in some Scolebythidae.

*Propodeum.* Brothers (1975) pointed out that the metathoracic-propodeal suture was completely obliterated ventral to the endophragmal pit but discernible dorsally in the chrysidoids examined by him. This is an apomorphy appearing six times on his cladogram. The state also obtains in the chrysidoid families he did not see, and so is autapomorphic for the superfamily.

The propodeum has probably accounted for most of the citations of Mesitiinae as transitional to Chrysididae (Ashmead, 1902; Reid, 1941; Moczar, 1970; Koenigsmann, 1978; Rasnitsyn, 1980). In Mesitiinae, as in most chrysidids, the propodeum bears spiniform projections on the lateral angles. These projections are apomorphic, and are the most significant feature linking mesitiines to chrysidids. Other characters suggested as being similar in the two groups cannot bear interpretation as synapomorphies: The reduced venation of mesitiines (three closed cells with the marginal cell more or less open) shows the same pattern as various cleptines and amisegines, groups to which they have most often been likened (Ashmead, 1902; Moczar, 1970). However, this pattern is not the groundplan of the Chrysididae, as discussed above, nor of Amiseginae (cf. figs. in Krombein, 1957). The integument structure (Koenigsmann, 1978) is not relevant; Mesitiinae do not have metallic coloration (Nagy, 1969; it is variable in chrysidids anyway) and the punctuation is no coarser in mesitiines than other bethylids such as *Pristocera* (and is also variable in chrysidids). Of the thoracic characters discussed by Reid (1941), the longitudinal furrow of the pronotum appears in numerous unrelated groups (cf. figs. in Reid, 1941), as is true of the furrows of the propodeal dorsum. A separate epicnemium with the sclerites ventrally in contact is primitive in Aculeata (Brothers, 1975). Rasnitsyn (1980) questioned this (and incorrectly referred to these sclerites as the postspiracular), but as documented in Richards (1977) this is primitive in Hymenoptera as a whole. The spiniform

projections are therefore the only "transitional" feature, the other characters mentioned being either plesiomorphies, which are inconsequential, or highly variable characters of little weight. Bohart and Kimsey (1982) apparently did not consider these projections as a groundplan characteristic of Chrysididae. This might be incorrect; spiniform armature does not occur in Loboscelidiinae and various Amiseginae (Krombein, 1957), which are treated as sister-groups in Bohart and Kimsey's cladogram, but some type of projection from the lateral angles is otherwise rather general in the family. However, even if spiniform projections are a shared apomorphy of mesitiines and chrysidids, this is most parsimoniously treated as convergent in light of the characters mesitiines share with other bethylids.

### *Metasoma*

*Number of visible segments.* Internation of the seventh metasomal tergum of the female is one of the outstanding autapomorphies of the Sphecoidea + Vespoidea (Aculeata s. str.) (Oeser, 1961; Brothers, 1975). Seven visible metasomal segments is the usual condition in Chrysoidea, although the seventh may be somewhat reduced. Thus, internation of the terminal segments in both sexes and development of the telescoping ovipositor tube is a primary autapomorphy of the Chrysididae. There are four visible terga in the female and five visible in the male in the groundplan, the state found in Cleptinae and Amiseginae. Further segments are retracted in other subfamilies, and failure to appreciate that this is part of a transformation series starting with the four/five condition is perhaps partly responsible for the confusion over the definition of the Chrysididae and its constituent taxa over the past century (documented in Reid, 1941; Krombein, 1957; Day, 1979). This has only been settled recently (Day, 1979). On the cladogram of Bohart and Kimsey (1982) the series is four-three-two in females, and five-four-three-two in males. These transformations define various components of the cladogram, but it should be noted that the states are not optimally distributed in their rendition. The metasomal internation states appear multiple times unnecessarily; the four/five condition appears twice when in fact it is characteristic of the entire family, and three visible terga in the male also appears twice.

*Articulation between sternum I and II.* The relationship between the first and second metasomal sterna provides critical characters for Rasnitsyn's (1980) system of Aculeata. Apart from the supposed synapomorphy described previously for his Embolemidae + (Bethylidae + Chrysididae), displacement of this articulation to the second tergum is one of the important characters for his Scoliidea. Rasnitsyn is the first author to have investigated the characters associated with this articulation, but has failed to demonstrate his putative synapomorphies. The apomorphy in Chrysoidea is a thick, straight sternum I butt-joined to II, and a straight margin to II with small lateral notches, invaginated edges and small desclerotized areas posterior to the invaginations. The plesiomorphic alternative is a thin, rounded sternum I overlapping II, and II straight but without invaginated edges, and notches if present medial. Rasnitsyn considered the Chrysididae to be further derived, with a thin margin to I consisting of membranous lobules overlapping II, and II with the desclerotized areas expanded onto the anterior margin so that it is deeply notched, with

the invaginations reduced but the rudiments discernible in Adelphinae (=Amiseginae). Actually this calls into question the homology. The interpretation can only be upheld on the basis of other characters, for it is not due to any intrinsic similarity. As discussed elsewhere in this paper, none of the other characters adduced by Rasnitsyn for grouping embolemids with Bethyidae + Chrysididae are acceptable synapomorphies, and they conflict with characters establishing the cladogram of Figure 4. Further, there does not appear to be any special similarity between Embolemidae and Bethyidae. Embolemids in fact have sternum I as thin as succeeding sterna, and it actually overlaps sternum II much as in other Chrysoidea (cf. especially the nearctic *Ampulicomorpha*, not discussed by Rasnitsyn, with Scolebythidae and Plumariidae). The resemblance between embolemids and bethylids is no more pronounced than that between chrysidids and those dryinids with a lobate sternum I (various gonatopodines in addition to Aphelopinae mentioned by Rasnitsyn). These characters do not appear to be useful in associating taxa. It may be added that this is also the case where Rasnitsyn discusses the sterna in Scolioidea; the supposed autapomorphy does not characterize all of the Scolioidea, and is found in other groups (vespids and formicids).

*Sting.* The terminology employed here is primarily that of Snodgrass (1933), used by Oeser (1961), Richards (1977), Evans et al. (1979) and Rasnitsyn (1980). The terminology of Smith (1970) is also given, as that was employed by Brothers (1975).

*Articulation within second valvifer.* The presence of a postincision (incisura postarticularis of Oeser), a dorsoventral constriction within the second valvifer (section 1 of gonocoxite IX) is one of the primary autapomorphies of the ovipositor of the Aculeata (Oeser, 1961; Brothers, 1975; Koenigsmann, 1978; Rasnitsyn, 1980). It divides the valvifer into dorsal and ventral arms (oblong plate and lamina falcata). Other Hymenoptera lack this, and along with other characters of the female terminalia such as loss of cerci and tergum VIII apophyses, this firmly establishes the monophyly of the Aculeata. Chrysoidea are further apomorphic in having this constriction divided by an articulation (Figs. 17, 22, 23). This is universal in the group (Oeser, 1961; Brothers, 1975; Rasnitsyn, 1980), including Plumariidae (Brothers, 1974, 1975) and verified by dissection of a female in the collection of the U.S. National Museum), and is thus a perfectly consistent autapomorphy.

*Furcula.* Oeser (1961) treated presence of a furcula (Figs. 17, 18, 23), the detached basal part of the second valvulae (notum of gonapophyses IX), as an autapomorphy of the Aculeata. This interpretation was followed by subsequent authors until Rasnitsyn (1980). Observing that the furcula is absent in Sclerogibbidae, Embolemidae and Dryinidae (Fig. 22), as well as some ants, Rasnitsyn suggested that development of this sclerite may have been a tendency in Aculeata rather than a character of the common ancestor. The sclerite is of diverse form in aculeates (figs. in Hermann and Chao, 1983). Typically it is tripartite, with ventral arms articulating with the second valvulae (Fig. 18), but it may be differently shaped, and certainly has been lost in Formicidae (cf. Hermann and Chao, 1983). However, it is most parsimonious to regard the structure as present in the groundplan of aculeates. Oeser (1961:fig. 41) illustrated a structurally simple "furculaähnliche" sclerite at the base of the second valvulae in some ichneumonoids and evanioids, and Hermann and Morrison (1979)

described a furcula in the ovipositor of a braconid. The latter authors concluded that the furcula arose prior to the origin of aculeates, for otherwise it "has had a polyphyletic origin." Ichneumonoida should be further investigated with respect to the structure of their supposed furcula. They are the sister-group of Aculeata (Mason, 1986b), and if a furcula is indeed widespread in the group, it must be inferred to have been present in the common ancestor of the Aculeata—where it was a primitive trait. Even if it should turn out that a furcula is a convergent development in some ichneumonoids, considering the generality of this sclerite in aculeates, it is still parsimonious to treat it as an ancestral aculeate character.

Following this interpretation, absence of a furcula is therefore a synapomorphy for the sclerogibbids, embolemids and dryinids. This is supported by the similar basal elongation of the second valvulae into a process in the three families (Figs. 19–22; cf. Rasnitsyn, 1980:figs. 147b, e, f). Rasnitsyn noted the similarity of embolemids and dryinids in this character, but argued that in Embolemidae the process was compressed into a "vertical lamella resembling the unpaired part of the furcula in Bethylidae." However, elsewhere he cited the formation as a synapomorphy of dryinids and sclerogibbids, "even though the process thus formed differs in shape in the two groups." Based upon my own dissections, the differences between dryinids and sclerogibbids are no greater than those between these families and embolemids. The supposed similarity of embolemids to bethylids is *ad hoc*; it is only a necessary inference given Rasnitsyn's grouping of embolemids, bethylids and chrysidids. Dryinids and sclerogibbids are no less similar to bethylids, but more important, are essentially the same as embolemids. A synapomorphy for Sclerogibbidae + (Embolemidae + Dryinidae) is the best conclusion with regard to the absence of the furcula.

*Articulation between second valvulae and valvifer.* The second valvifers (gonocoxites IX) articulate with the second valvulae (gonapophyses IX; sting) via a pair of articular processes at the base of the valvulae (Figs. 17, 22) in most Hymenoptera including Aculeata. As noted by Oeser (1961), Bethylidae and Chrysididae lack a functional articulation. The proximal arm of the second valvifer is well separated from the base of the valve (Fig. 23; Oeser, 1961:figs. 47, 102; Rasnitsyn, 1980:figs. 147c, d). This is synapomorphic for the two families, as Rasnitsyn (1980) realized. Both groups possess further modifications. Chrysididae have most parts of the sting reduced, and function is lost in some groups. Some Bethylidae have a secondary articulation between the distal arm of the second valvifer and second valvulae via elongate processes from the valvifer (*Cephalonomia*, Oeser, 1961; *Bethylus*, Rasnitsyn, 1980). These further apomorphies are not general (*Pristocera*, Fig. 23, and *Pilomesitius* lack the secondary articulation; and the sting of most chrysidids has not been described in much detail).

#### *Life history*

*Hosts and habitats.* Rasnitsyn (1980) believed prey searching within the substrate ("probably of beetle larvae in decayed wood") to be the primitive condition in Aculeata, and indeed, it is widespread in diverse groups. In Chrysidoida, most bethylids do attack beetle larvae (e.g., list in Evans, 1978), and the hosts of *Ycaploca*

(Scolebythidae) are probably wood-boring cerambycids (Brothers, 1981). Other scolebythids have been collected in wood (Evans et al., 1979), and plumariid females are hypogaecic (Evans, 1966). Chrysidids have diverse hosts, but these are attacked at stages where they are leading a "confined existence" (Rasnitsyn, 1980). The hosts range from tenthredinoid larvae (Cleptinae) to phasmid egg cases (Amiseginae + Loboscelidiinae) to aculeate larvae (most members of the remaining subfamilies). Sclerogibbidae attack Embiidina, certainly an autapomorphy. Embolemidae have been reared from nymphs of a fulgoroid living in rotting wood (Bridwell, 1958). Finally, Dryinidae attack a variety of Homoptera Auchenorrhyncha, mostly free-living Fulgoroidea and Cicadellidae (see list in Olmi, 1984).

The shared host taxon of embolemids and dryinids is here considered a synapomorphy. Rasnitsyn (1980) denied this interpretation. He considered embolemids' "similarity to Bethylidae and Chrysididae with regard to the habitat of their hosts" to be "as important as the taxonomic closeness of the hosts of Embolemidae and Dryinidae." Further, he treated active, non-Holometabola hosts as a synapomorphy between Dryinidae and Sclerogibbidae. These tenuous homologies are quite incredible; by Rasnitsyn's own interpretation the host habitat shared by Embolemidae, Bethylidae and Chrysididae is plesiomorphic. The embiid nymphs attacked by Sclerogibbidae are no more free-living than the achilid nymphs attacked by Embolemidae. And non-Holometabola is scarcely acceptable as a synapomorphic host group if Homoptera Auchenorrhyncha is not.

*Endoparasitism.* Most Dryinidae share a highly distinctive life history (summary in Olmi, 1984). The first larval instar is endoparasitic, but later instars protrude from the host as a cyst formed by cast exuviae. In Aphelopinae, at least the first instar is surrounded by a hypertrophied mass of host tissue, the trophamnion (Olmi, 1984). This persists until the final larval instar, but the second instar protrudes through this to form the cyst of exuviae, although it is of different texture from that of other dryinids (Olmi, 1984). This cyst is certainly apomorphic, and embolemids have a similar state. Bridwell (1958) described a "translucent, rounded mass" protruding from the host of *Ampulicomorpha confusa*, and R. A. Wharton (*in litt.*) also observed a protruding sac while rearing this species. The origin of the sac was not determined in these cases, and may have been formed by host tissue. This is little different from Aphelopinae, and both families are further similar in pupation in a cocoon formed away from the host.

Rasnitsyn (1980) characterized the life history of Embolemidae as "completely endoparasitic," and stated that this "finds its analogy among Aculeata only in Chrysididae, but not in Dryinidae." Although Bridwell's wording is somewhat ambiguous, this author stated that the biology of *A. confusa* "is in all essential particulars a dryinid biology," and this is also concluded by R. A. Wharton (*in litt.*). Rasnitsyn's statements contain another error. The reference to an endoparasitic chrysidid is apparently to *Chrysis neglecta* (Maneval, 1932; now placed in *Spinolia*), but this species is reported to be external during the first instar. A more "completely endoparasitic" development is found in a dryinid, *Aphelopus* (now *Crovettia*; Olmi, 1984) *theliae*, a polyembryonic parasitoid without any external sac. Embolemids and dryinids have the same basic life history, which is a synapomorphy.

## DISCUSSION

Most of the groups of the cladogram resulting from this study (Fig. 4) are supported by more than one character, as shown in the section on groundplan diagnoses. The features discussed are generally consistent, even the characters of the wing venation. The only component apparently problematic is (Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae). The only problematic term is Dryinidae. Both groups are supported only by homoplasious characters, which show convergent development in other groups. The arrangements suggested here based on the homoplasious characters are most parsimonious when all characters are considered. For the characters of the component, reduction of the labial palpi has also occurred in Plumariidae, and constriction of the metapostnotum within Scolebythidae. Plumariids are excluded from the component by the venational characters uniting Scolebythidae with the remaining five families, as well as their plesiomorphic metapostnotum. Scolebythids are excluded by the palpal character, and an unconstricted metapostnotum is found in *Ycaploca*. Only one autapomorphy has been identified for Dryinidae, and reduction of the fore wing venation to five closed cells occurs in several other groups. However, as discussed above, it is not part of the groundplan of these latter groups. The remaining components and terms are all supported by unique features. Therefore this cladogram may be regarded as quite strong overall.

Of the relationships established here, that between Plumariidae, Scolebythidae and the component formed by the remaining families is the same as that suggested by Brothers (1975:fig. 2) for Plumariidae, Scolebythidae and his "bethylid group," despite some changes in character state interpretations. Brothers' final cladogram (Fig. 1) was different, but he did not see all the taxa nor was this based on analysis. Koenigsmann (1978) grouped Embolemidae and Dryinidae, the traditional concept strongly corroborated here, but his other suggested relationships (Fig. 2) are rejected in this study. Koenigsmann considered all the chrysidoid families, but drew his data from a literature survey and did not attempt a comprehensive treatment of all the characters he mentioned. Partly as a result, several of his character interpretations are unacceptable. Sclerogibbidae were removed from Aculeata based on presumed primitive antennae, but as shown in this paper this must be considered a reversal. As for his suggested relationship of Plumariidae + Scolebythidae based on loss of the pronotal collar, as Brothers mentioned and as is discussed above, the states in these two families are actually different.

The relationship established between Sclerogibbidae and Embolemidae + Dryinidae was previously unsuspected, but that between the latter two families, and Bethylidae + Chrysididae are inveterate views. Rasnitsyn (1980) accepted the last group, but otherwise proposed a very different system (Fig. 3). As discussed in the preceding section, his system is unsupportable even on the basis of the characters used in establishing it. Although using cladistic terms, he frequently grouped by symplesiomorphy, or trends not groundplan characters. Several of his synapomorphies are dubious homologies, or do not characterize all members of the groups based on them. This is partly due to his rejection of cladistic methods; he was thus unable to properly evaluate the informativeness of his characters. And partly it is due to his use of fossil taxa as recognized ancestors in ancestor-descendant relationships, a

fallacious procedure (Hennig, 1966; Engelmann and Wiley, 1977). For Aculeata, Rasnitsyn considers the Jurassic Bethylonymidae as the ancestor, even though it had an external ovipositor and multisegmented antennae (that is, possessed none of the aculeate autapomorphies). In his discussion of the metasternum, although he apparently could not see the metasternum on his specimens of this taxon, he stated that a metasternal "platform" was "probably not developed as yet" and thus is a derived feature in extant taxa. This is one of the crucial characters of his system, and many of his *ad hoc* interpretations of other characters are necessary to conform to it. Although his work presented new data, in general it must be reanalyzed before it is of any use in phylogenetic inference. Where I have done so his interpretations are not upheld.

In conclusion, it is worth emphasizing that one of the reasons cladistics has had great impact on systematics is that there is a strong relationship between evidence and hypothesis. Groups can only be recognized on the basis of characters, not general resemblance. This study has built on previous work, but has been more comprehensive in that more evidence has been adduced and analyzed. The result (Fig. 4) is correspondingly better able to account for the available evidence, and so is the best present hypothesis of the phylogenetic relationships of the Chrysidoidea.

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## LIST OF TAXA EXAMINED

The taxa examined were selected to maximize diversity of higher categories represented. In the four smaller chrysidoid families all available species were studied, whereas for the three larger families emphasis was at the generic level. Survey of outgroups was by exemplar taxa, with particular attention to Ichneumonoidea (Doryctinae, Helconinae and Pimplinae) and Sphecidae (Sphecinae). The specimens are deposited in the collections of the U.S. National Museum and the Museum of Comparative Zoology.

## PLUMARIIDAE

*Plumarius* sp. (female and male)  
*Plumaroides andalgalensis*  
*Myrmecopterina okahandja*

*Scolebythus madecassus*  
*Ycaploca evansi*

## SCOLEBYTHIDAE

*Clystopsenella longiventris*

## SCLEROGIBBIDAE

*Probethylus callani*  
*mexicanus*

*schwarzi*  
sp.  
*Sclerogibba citipes*  
*magrettii* ?  
*taprobanana*  
spp.

## EMBOLEMIDAE

*Ampulicomorpha confusa*  
sp.  
*Embolemus nearcticus*  
*ruddii*  
spp.

## DRYINIDAE

## APHELOPINAE

*Aphelopus albopictus*  
*bicolor*  
*diffusus*  
*maculiceps*  
*melaleucus*  
*nigriceps*  
*orientalis*  
*rufiventris*  
*varicornis*  
*Crovettia theliae*  
sp.

## ANTEONINAE

*Anteon ephippiger*  
*flavicornis*  
*gaullei*  
*jurineanum*  
*puncticeps*  
*scapulare*  
spp.

*Deinodryinus asiaticus*  
*atriventris*  
spp.

*Lonchodryinus ruficornis*  
sp.

## BOCCHINAE

*Bocchus flavicollis*  
*mirabilis*  
*richardsi*  
*robustus*  
*rubricus*  
*Mirodryinus xerophilus*

## THAUMATODRYININAE

*Thaumatotdryinus* sp.

## GONATOPODINAE

*Acrodontochelys americanus*  
*Apterodryinus citrinus*  
*secundus*  
*Dicondylus perkinsi*  
*Echthrodolphax hortusensis*  
*Esagonatopus niger*  
*Gonatopus breviforceps*  
*daunus*  
*ombrodes*  
*subtilis*  
*Haplogonatopus apicalis*  
*hernandezae*  
*Neodryinus koebelei*  
*trinitatis*  
*Neogonatopus fentoni*  
*Pseudogonatopus albosignatus*  
*hospes*  
*ortholabis*  
*sarawaki*  
*sjoestedti*  
spp.  
*Tetrodontochelys anomalus*  
*obscurus*  
*plesius*  
*unicus*  
*Trichogonatopus albomarginatus*

## DRYININAE

*Dryinus alatus*  
*antilleanus*  
*browni*  
*lankanus*  
*pulcher*  
*stantoni*  
*surinamensis*  
*Richardsidryinus erraticus*  
*Trydryinus gibbosus*  
*poecilopterae*  
*ruficauda*  
*ruficeps*

## BETHYLIDAE

## MESITIINAE

*Anaylax aegyptius*  
*Clytrovorus horvathi*  
*Codorcas cursor*  
*Mesitius apterus*  
*ghilianii*

*spathulifer*  
 sp.  
*Metrionotus egypticus*  
*Pilomesitius madagascarensis*  
*Sulcomesitius africanus*  
*brevidens*  
*consimilis*  
*krombeinii*  
*rieki*  
*szentivanyi*  
*vechti*  
*vietnamensis*

## PRISTOCERINAE

*Apenesia amazonica*  
*malaitensis*  
*Dicrogenium* sp.  
*Dissomphalus punctatus*  
*xanthopus*  
*Neodicrogenium* sp.  
*Parascleroderma nigrum*  
*Pristocera armifera*  
*depressus*  
*japonica*  
*Prosapenesia lacteipennis*  
*Pseudisobranchium albipes*  
*pallidipes*  
*subcyaneum*

## EPYRINAE

## EPYRINI

*Acanthepyris* sp.  
*Allepyris* sp.  
*Anisepyris aurichalceus*  
*tlaloc*  
*Bakeriella flavicornis*  
*inca*  
*Calyoza* sp.  
*Calyozina mexicana*  
*Epyris amabilis*  
*dodecatomus*  
*extraneus*  
*niger*  
*rufipes*  
*Holepyris crenulatus*  
*remotus*  
*sylvanidus*  
*Laelius centratus*  
*Pristobethylus* sp.  
*Rhaddepyris apache*

*gracilis*  
*luteipennis*  
*platycephalus*  
*viridissimus*

## CEPHALONOMIINI

*Cephalonomia conophthori*  
*formiciformis*  
*Israelius carthami*  
*Plastanoxus chittendenii*

## SCLERODERMINI

*Chilepyris herbsti*  
*Glenosema crandalli*  
*silvicola*  
*Nesepyrus virginianus*  
*Nothepyris brasiliensis*  
*Sclerodermus cereicollis*  
*macrogaster*  
 sp.  
*Thlastepyrus pertenuis*

## BETHYLINAE

## BETHYLINI

*Bethylus amoenus*  
*arcuatus*  
*decipiens*  
*fuscicornis*

## SIEROLINI

*Eupsenella agilis*  
 sp.  
*Goniozus aethiops*  
*carborum*  
*silvestris*  
*spilogaster*  
*Lytopsenella herbsti*  
*Prosierola lata*  
*variegata*  
*Sierola koa*

## CHRYSIDIDAE

## CLEPTINAE

*Cleptes afer*  
*alienus*  
*consimilis*  
*moczari*  
*nitidulus*  
*rufifemur*  
*scutellaris*  
*semiauratus*  
*speciosus*

*Cleptidia aurora*  
*mutilloides*

#### LOBOSCELIDIINAE

*Loboscelidia bakeri*  
*cervix*  
*collaris*  
*dejecta*  
*nigra*  
*philippinensis*  
*reducta*  
*rufa*  
*scutellata*

#### AMISEGINAE

*Adelphe anisomorphae*  
*mexicana*  
*Amisega cooperi*  
*Mesitiopterus evansi*  
*floridensis*  
*kahlii*  
*townsendi*  
*Microsega bella*  
*Myrmecosega bispinosa*  
*Myrmecomimesis nigricans*  
*Nesogyne taino*

#### PARNOPINAE

*Parnopes chrysoprasinus*  
*concinus*  
*denticulatus*  
*edwardsii*  
*fischeri*  
*fulvicornis*  
*grandior*

#### ELAMPINAE

*Elampus gayi*  
*viridicyaneus*  
*Hedychrydium dimidiatum*  
*fletcheri*  
*roseum*  
*Hedychrum nobilis*  
*Holypyga fervida*  
*gloriosa*  
*ventralis*  
*Omalus aeneus*  
*auratus*  
*telfordi*  
*variatus*

#### ALLOCOELIINAE

*Allocoelia capensis*

#### CHRYSIDINAE

##### CHRYSIDINI

*Argochrysis mesillae*  
*Ceratochrysis cyanosoma*  
*enhuycki*  
*kansensis*  
*perpulchra*  
*quadrituberculata*  
*Chrysis austrialia*  
*antennalis*  
*coerulans*  
*fuscipennis*  
*gibba*  
*ignita*  
*intricata*  
*japonica*  
*megacephala*  
*nitidula*  
*smaragdula*  
*splendens*  
*viridula*  
*Chrysura austriaca*  
*cobaltina*  
*cuprea*  
*inuitata*  
*pustulosa*  
*Chrysurissa densa*  
*Pyria lyncea*  
*oculata*  
*stilboides*  
*Trichrysis cyanea*  
*doriae*  
*lusca*  
*tridens*

##### EUCHROEINI

*Euchroeus purpuratus*  
*Ipsiura neolateralis*  
*Neochrysis bruchi*  
*carina*  
*panamensis*  
*Pseudospinolia neglecta*  
*tetrini*  
*Stilbum cyanurum*  
*splendidum*  
*viride*